PHYLOGENETIC IMPLICATIONS OF THE EXISTENCE
OF TWO MODERN GENERA OF BATHYERGIDAE
(MAMMALIA, RODENTIA)
IN THE PLIOCENE SITE OF LANGEBAANWEG (SOUTH AFRICA)

By

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(With 7 figures and 4 tables)

ABSTRACT

The oldest known *Bathyergus* and *Cryptomys* are found together in the Langebaanweg 'E' Quarry site of the Varswater Formation in Cape Province (South Africa). They are represented by two previously unrecorded species: *Bathyergus hendeyi* sp. nov. and *Cryptomys broomi* sp. nov. These species are characterized by primitive characteristics and may represent ancestors of the extant species. Their affinities with modern Bathyergidae, especially *Georychus capensis* and the fossil *Gypsorychus*, are discussed in the light of new chromosomal and electrophoretic data. The fossils provide some calibrations and arguments to the molecular hypotheses.

CONTENTS

INTRODUCTION

Bathyergidae are hystricognathous rodents characterized by a digging mode of life and are endemic to the African continent. Until recently, their systematic position has remained very controversial. However, Maier & Schrenk (1987), in an ontogenetic study of the development of the masseteric muzzle, demonstrated their position among hystricomorphous rodents. This has confirmed the previous work of Lavocat (1973) on Miocene fossils.

Modern South African Bathyergidae are represented by three endemic genera that were separated into two subfamilies by Roberts (1951) on the basis of morphometric characteristics. These are the subfamily Bathyerginae, which includes the genus *Bathyergus*, and the subfamily Georychinae, which includes

265

the genera *Georychus* and *Cryptomys*. This division of the family was partly supported by Nevo *et al.* (1987), who concluded that there was need of urgent revision of the taxonomic status of these rodents.

In their general discussion of the genetic distance extrapolated from allozyme differentiation between the genera, Nevo *et al.* (1987) proposed two different hypotheses concerning the phylogenetic relationships and the origins of cladogenesis among these genera (Fig. 1). Both clusters agree in giving a divergence age between *Bathyergus janetta* and *B. suillus* and between *Cryptomus h. natalensis* and *C. h. hottentotus* of around 2.5 Ma, but there are still problems relating to earlier divergences of some taxa (Fig. 1). The difficulty arises from the intermediate position of *Georychus*. In the first cluster, *Georychus* is considered as the sister-genus of *Cryptomys*, being closer to *C. damarensis* than to *Bathyergus*. This leads to the first hypothesis of a differentiation of *Bathyergus* (Bathyerginae) at 12 Ma, and a cladogenesis of *Cryptomys* and *Georychus* (Georychinae) at about 5 Ma (Fig. 1A). In the second hypothesis, Nevo *et al.* (1987) suggested that *Georychus* is the sister-genus of *Bathyergus*, and is farther away from *Cryptomys*. The latter hypothesis is in contradiction to Roberts's (1951) classification and implies that the divergence between *Bathyergus* and *Georychus* occurred around 8 Ma, and that *Cryptomys* appeared more recently at around 4.5 Ma (Fig. 1B). The study of mitochondrial DNA variation among bathyergid rodents also shows closer affinities between *Bathyergus* and *Georychus* than between *Bathyergus* and *Cryptomys* (Honeycutt *et al.* 1987).

These two hypotheses suggest that around 4–5 Ma there was probably a major phase of differentiation among the three modern South African genera. According to the first hypothesis, there is a differentiation among the three modern South African genera. The first hypothesis suggests a differentiation of *C. damarensis* and *Georychus* at this date; and the second hypothesis suggests an early differentiation between *C. damarensis* and other species of *Cryptomys*. If either of these hypotheses is true, it should be possible to find some trace of the purported events in the fossil record.

The bathyergid fossil record is poor but the family is well known in East and South Africa from lower Miocene times (about 20 Ma). The family is represented in South Africa by three extinct genera whose affinities have been discussed by Lavocat (1973). *Bathyergoides* is known from 20 to 14 Ma and represents a primitive form not related to the modern genera. *Proheliophobius* is found at the same time and, according to Lavocat (1973), could represent a good ancestor to *Heliophobius*, *Georychus* and *Cryptomys*. The most recent genera, *Paracryptomys* and *Richardus* (14 to 12 Ma), could be the direct ancestors of *Cryptomys* and *Heterocephalus* (Lavocat 1973, 1989). There is no record of bathyergids in the upper Miocene times due to a general gap in the fossil record of tropical Africa.

The lower Pliocene sites are, in general, poorly documented for rodents both in East and South Africa, except for the Langebaanweg site (Cape Province, South Africa) in the Varswater Formation. This site is famous for having yielded numerous, well-preserved fossil vertebrates, which include thousands of rodents. Langebaanweg is estimated at around 5–4.5 Ma (see discussion in Hendey 1981), and it has yielded an important assemblage of Bathyergidae. The excavations have shown at least two different and important strata (Hendey

1981): the Quartzose Sand Member (QSM) at the base of the formation, and the Pelletal Phosphorite Member (PPM), which includes beds 3AS and 3AN. Both levels date from the Pliocene, and have different faunas, although Hendey (1981) has suggested that a very short time period occurred between the deposition of the two members.
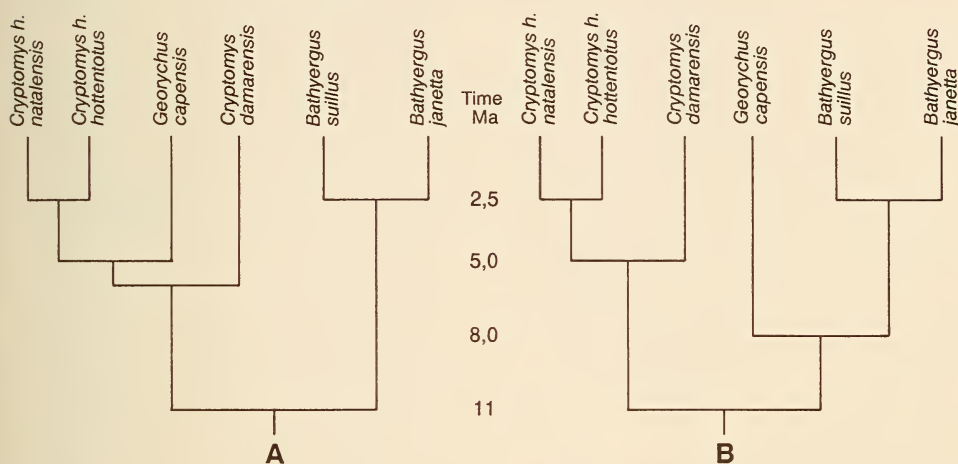

Fig. 1. Summary of the two phylogenetic hypotheses proposed by Nevo *et al.* (1987) from chromosomal and electrophoretic data on modern Bathyergidae from South Africa. The main differences between the hypotheses concern the affinities of *Georychus capensis* and its age of divergence. A. *Georychus* is closest to *Cryptomys* and has recently diverged (about 5 Ma). B. *Georychus* is closer to *Bathyergus* and was differentiated earlier (about 8 Ma).

In a preliminary study of the rodent material from 'E' Quarry at Langebaanweg, Pocock (1976) reported two bathyergids—*Bathyergus* sp. and *Cryptomys* sp. This author examined only one level (QSM), and the material was simply listed and not described or further identified. Re-examination of specimens at the South African Museum from the QSM and description of supplementary material from the PPM have shown that Bathyergidae are the most abundant rodents of the 'E' Quarry site at Langebaanweg. They are very well represented in the QSM and also in the PPM members, reaching 80 per cent of the total rodents in the PPM 3AN member. The morphological study of these fossils and their comparison with modern equivalents should provide some indication of the relationships among modern genera, as well as those of the Miocene, and should provide further evidence on the relationships of *Georychus*.

A systematic study of the Langebaanweg Bathyergidae has been undertaken in order to test the two evolutionary hypotheses of Nevo *et al.* (1987), and to try to determine the polarity of the characters. Comparisons between fossil and modern forms have been made through examination of the collections of the Transvaal Museum (TM), the Bernard Price Institute at the University of the Witwatersrand, Johannesburg (BPI), the South African Museum (SAM), the Natural History Museum of Paris (MNHN), the Natural History Museum, London (BMNH), and the Los Angeles County Museum (LACM).

SYSTEMATIC STUDY

Family **Bathyergidae** Waterhouse, 1841

Genus *Bathyergus* Illiger, 1811

The dune molerat (*Bathyergus*) is represented in south-western Africa by two distinct extant species: *B. suillus* Schreber, 1782 (the Cape dune molerat) and *B. janetta* Thomas & Schwann, 1904 (the Namaqua dune molerat) (Meester *et al.* 1986). This distinction, based initially on the morphology, has been confirmed by chromosomal studies (Nevo *et al.* 1985) (*B. suillus* being characterized by 2N = 56 and *B. janetta* by 2N = 54). A local population containing smaller-sized individuals, *B. suillus intermedius* Roberts, 1926, from Klaver, Cape Province, has also been taken into consideration.

Few representatives of the genus *Bathyergus* have been recorded from the southern African Pliocene fossil record, and the species of *Bathyergus* from Langebaanweg is, at present, the earliest one. The family Bathyergidae is well represented in the Miocene times but by different genera whose affinities remain uncertain (Lavocat 1973). In the most recent Plio–Pleistocene cave deposits at Taung (North-West Province) and Makapansgat (Northern Province), a large bathyergid of unknown affinities, *Gypsorychus* Broom, 1934, has been described. An undescribed skull of *Bathyergus* has also been recorded at the Upper Pleistocene site of Elandsfontein (De Graaff 1981—1–0.3 Ma).

Bathyergus hendeyi sp. nov.
Figs 2, 3A–D, 4–6

Bathyergus hendeyi sp. nov. is a large bathyergid that is the most abundant of the Langebaanweg rodent assemblages. It is characterized by the existence of 2–4 cheek-teeth, depending on the age of the individual. As in modern species of *Bathyergus*, the upper incisors have a median groove separating them in two at their tip, and the lower incisors are ungrooved. The upper incisors do not extend behind the tooth row as in *Georychus* and, according to Meester *et al.* (1986), the angular portion of the mandible is produced to well behind the occipital condyles, as in modern *Bathyergus* species.

Etymology

The species is named in honour of Dr Q. B. Hendey, who devoted his time to the Langebaanweg excavations and studied many large mammals from this site.

Material

Holotype. SAM–PQL20402 in the South African Museum (Cape Town). Anterior skull fragment with left and right DP⁴–M³, from the Quartzose Sand Member (QSM) of the Varswater Formation in 'E' Quarry, Langebaanweg (Figs 2C–E, 3A, 3C).
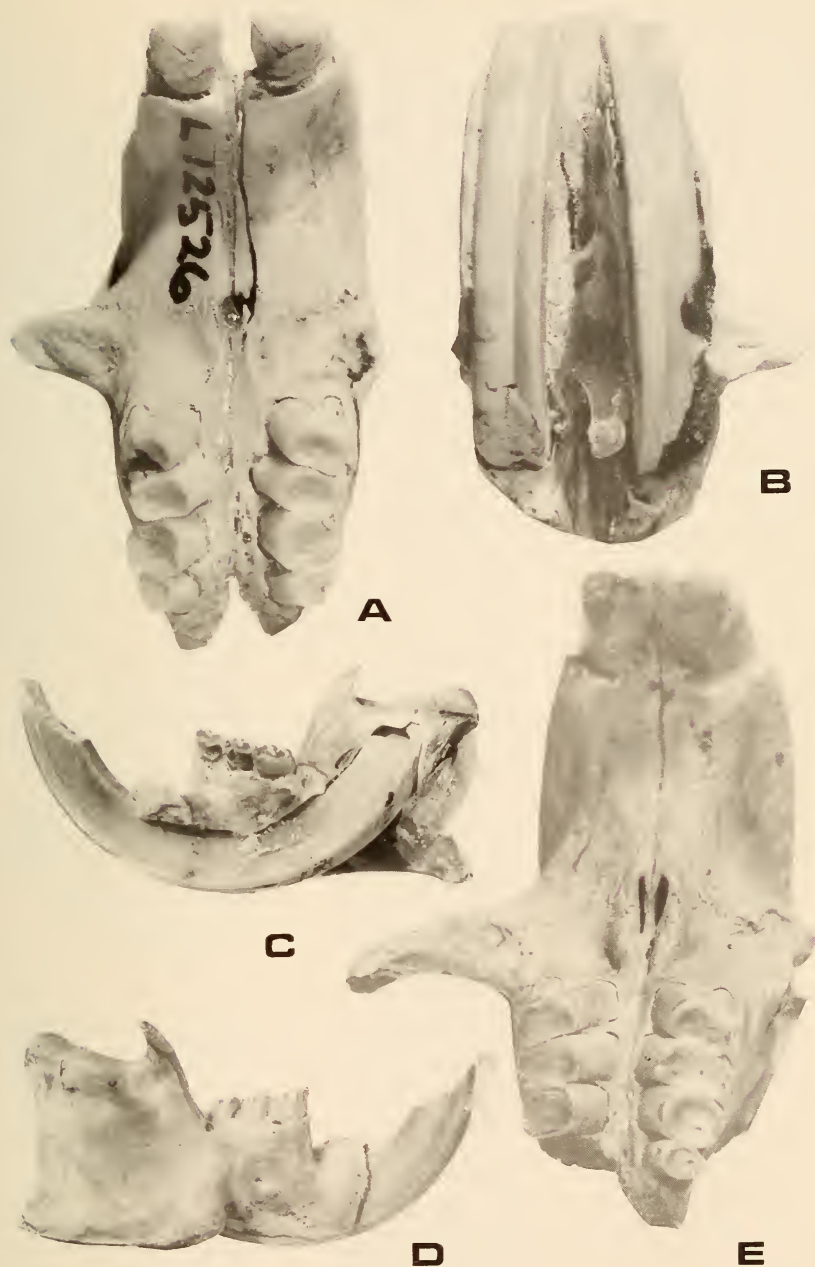
Fig. 2. *Bathyergus hendeyi* sp. nov. A–B. Skull, SAM–PQL12526 from Langebaanweg
PPM 3AS member. A. Ventral view of anterior skull fragment (× 2.6). B. Dorsal view
(× 1.5). C–E. Skull and mandible, SAM–PQL20402, holotype, from Langebaanweg QSM
member. C. Internal view of right mandible (× 2.8). D. External view of mandible
(× 2.8). E. Ventral view of anterior skull fragment with upper dental rows (× 1.5).

Skull fragments

QSM: SAM–PQL28388, anterior skull fragment with left and right DP^4–M^3.

PPM 3AN: SAM–PQL63443, anterior skull fragment with left DP^4–M^3.

PPM 3AS: SAM–PQL12526 (Fig. 2A, B), anterior skull fragment with left and right DP^4–M^3.

Mandible fragments

QSM: 11 right and 9 left mandible fragments with DP$_4$–M$_3$; 49 right and 72 left mandible fragments with DP$_4$–M$_2$; 27 right and 34 left mandible fragments with DP$_4$–M$_1$; 7 right and 6 left mandible fragments with DP$_4$; 2 right and 2 left mandible fragments with M$_{13}$; 4 right and 4 left mandible fragments with M$_{23}$; 6 right and 2 left mandible fragments with M$_1$; 4 right and 4 left mandible fragments with M$_2$; 1 left mandible fragment with M$_3$; 15 right and 14 left mandible fragments with M$_{12}$; 8 right and 18 left mandible fragments without teeth.

PPM 3AN: 7 right and 3 left mandible fragments with DP$_4$–M$_3$; 43 right and 27 left mandible fragments with DP$_4$–M$_2$; 22 right and 12 left mandible fragments with DP$_4$–M$_1$; 6 right and 5 left mandible fragments with DP$_4$; 2 right and 1 left mandible fragments with M$_{13}$; 24 right and 44 left mandible fragments with M$_1$; 19 right and 21 left mandible fragments with M$_2$; 46 right and 45 left mandible fragments with M$_{12}$; 108 right and 69 left mandible fragments without teeth.

PPM 3AS: 4 right and 4 left mandible fragments with DP$_4$–M$_3$; 17 right and 14 left mandible fragments with DP$_4$–M$_2$; 9 right and 8 left mandible fragments with DP$_4$–M$_1$; 2 right mandible fragments with DP$_4$; 3 right and 1 left mandible fragments with M$_{13}$; 1 left mandible fragment with M$_{23}$; 2 right and 2 left mandible fragments with M$_1$; 6 right and 4 left mandible fragments with M$_2$; 4 right and 3 left mandible fragments with M$_{12}$; 6 right and 12 left mandible fragments without teeth.

Upper tooth rows

QSM: 8 right and 4 left maxillary fragments with DP^4–M^3; 5 right and 4 left maxillary fragments with DP^4–M^2; 1 right and 7 left maxillary fragments with DP^4–M^1; 3 right and 5 left maxillary fragments with DP^4; 1 left maxillary fragment with M^{13}; 3 left maxillary fragments with M^{23}; 1 right maxillary fragment with M^1; 1 right and 4 left maxillary fragments with M^{12}.


Fig. 3 (*see facing page*). Teeth of specimens of Bathyergidae from Langebaanweg. A–D. *Bathyergus hendeyi* sp. nov. from QSM member. A. SAM–PQL20402, holotype. Left upper molar row with DP^4–M^3 ($\times$ 7.4). B. SAM–PQL13060/B, right mandible with DP$_4$–M$_3$ ($\times$ 7.4). C. SAM–PQL20402, holotype. Right mandible with DP$_4$–M$_3$ ($\times$ 7). D. SAM–PQL50230, isolated left DP$_4$ (up) and M$_1$ (down) ($\times$ 16).
E–F. *Cryptomys broomi* sp. nov. from QSM member. E. SAM–PQL25101, left dental row with DP$_4$–M$_3$ ($\times$ 14). F. SAM–PQL24012, holotype, left dental row, with DP$_4$–M$_3$ ($\times$ 13).
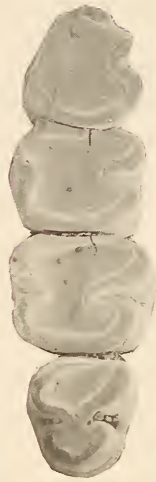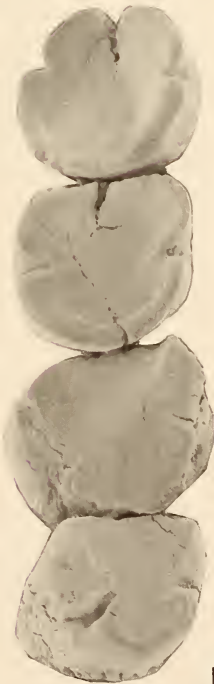
PPM 3AN: 1 left maxillary fragment with DP^4–M^3; 4 right and 2 left maxillary fragments with DP^4–M^2; 1 right and 1 left maxillary fragments with DP^4–M^1; 1 left maxillary fragment with M^{23}; 1 right and 1 left maxillary fragments with M^1; 1 left maxillary fragment with M^{12}; 1 left and 1 right maxillary fragments with M^2; 2 right and 2 left maxillary fragments without teeth.

PPM 3AS: 5 right and 1 left maxillary fragments with DP^4–M^3; 2 right and 2 left maxillary fragments with DP^4–M^2; 1 right and 3 left maxillary fragments with DP^4; 4 right and 2 left maxillary fragments with M^{23}; 1 left maxillary fragment with M^1; 1 right and 1 left maxillary fragments with M^{12}; 1 left maxillary fragment without teeth.

Diagnosis

Medium-sized *Bathyergus* with a relatively large infraorbital foramen and a wide angle between the zygomatic arch and the dental row; anterior part of skull high; low-crowned molars. Upper incisors reaching the level of M^{12} instead of DP^4–M^1 on modern *Bathyergus*; DP_4 rounded, not elongated.

Differentiated from *B. suillus* by the smaller size of skull and molars, especially of the DP_4, less rectilinear nasals, lower crowns, and narrower upper incisors. Differentiated from *B. janetta* by the slightly larger size of the skull and slightly smaller molars, lower crowns and wider upper incisors.

Description

Measurements are given in Tables 1 and 2.

Skull. Only anterior parts of skulls were found at Langebaanweg. The frontal region is high in lateral view and the upper incisors reach the level of the M^{12}. The nasals are enlarged posteriorly, whereas the muzzle is wide. The infraorbital foramen is wide and the zygomatic arch departure makes a right angle with the dental row (Fig. 2A, B, E).

Mandible. This species is characterized by a very important hystricognathous angle of the mandible and the close proximity of the symphysial joint to the DP^4. There is a relatively large space between the distal part of the dental row and the beginning of the coronoid process (Fig. 2C, D).

Teeth. Molars are described here but, as in all bathyergids, there is a large variation in the size and shape of the teeth that is age dependent (Taylor *et al.* 1985; Denys 1988) (Fig. 4).

Upper molars. The DP^4 is a square tooth comprising two lobes, each separated by an internal and an external sinus. These sinuses are only slightly invaginated towards the centre of the tooth; the labial invagination is deeper than the lingual one. In most cases these sinuses are invisible and the tooth appears round. The M^1 is more compressed antero-posteriorly than the DP^4 and has a rectangular shape. No internal or external sinuses are seen. The M^2 tooth is rounded and shows very slight sinuses. The DP^4, M^1 and M^2 are nearly equivalent in size, whereas the M^3 is the smallest tooth of the dental row and shows some variation in shape. It is sometimes round and unilobated; in other cases it is more elongated with a small posterior lobe; there is a trace of a small external sinus (Fig. 3A).

TABLE 1

Dental measurements (in mm) of *Bathyergus hendeyi* sp. nov. from Langebaanweg. Abbreviations: QSM—Quartzose Sand Member; 3AN and 3AS—Pelletal Phosphorite Member levels 3AN and 3AS, respectively; n—number of individuals; S.D.—standard deviation.

Tooth		QSM		3AN		3AS	
		Length	Width	Length	Width	Length	Width
DP^4	n	9		5		2	
	Minimum	1.83	2.68	1.96	2.5	1.83	3.08
	Maximum	2.17	3.5	2.13	3.29	2.15	3.1
	Mean	1.92	2.99	2.03	2.88	—	—
	S.D.	0.09	0.27	0.14	0.31	—	—
M^1	n	11		5		2	
	Minimum	1.29	2.42	1.79	2.42	1.93	3.42
	Maximum	1.92	4	2.17	3.25	1.96	3.5
	Mean	1.42	3.12	2.02	2.94	—	—
	S.D.	0.23	0.46	0.06	0.34	—	—
M^2	n	10		3		4	
	Minimum	2.04	2.41	2.08	2.33	2	2.88
	Maximum	2.5	3.33	2.38	2.92	2.67	3.42
	Mean	2.22	2.95	2.24	2.72	2.46	3.07
	S.D.	0.18	0.29	0.15	0.25	0.31	0.25
M^3	n	9		3		3	
	Minimum	1.67	1.92	1.83	1.96	1.67	2.08
	Maximum	1.9	2.71	2.08	2.5	1.92	2.33
	Mean	1.86	2.2	1.93	2.2	1.75	2.19
	S.D.	0.36	0.27	0.13	0.28	0.13	0.13
DP$_4$	n	22		21		10	
	Minimum	2.15	1.89	2.21	2.25	2.21	2.29
	Maximum	2.96	2.73	2.88	3.33	2.88	3
	Mean	2.44	2.31	2.62	2.69	2.62	2.57
	S.D.	0.18	0.18	0.18	0.27	0.21	0.21
M$_1$	n	22		25		11	
	Minimum	1.85	2	2	2	1.92	2.75
	Maximum	2.38	2.82	2.58	3.25	2.58	3.17
	Mean	2.12	2.43	2.32	2.64	2.32	2.99
	S.D.	0.15	0.21	0.15	0.35	0.23	0.15
M$_2$	n	15		22		11	
	Minimum	2	2.04	2.08	2.13	2.08	2.42
	Maximum	2.58	2.85	2.83	3.42	2.67	3.38
	Mean	2.27	2.51	2.49	2.8	2.42	2.9
	S.D.	0.15	0.29	0.19	0.39	0.2	0.35
M$_3$	n	3		7		7	
	Minimum	1.75	1.77	1.96	2.17	2.13	2.08
	Maximum	2	2.15	2.75	2.5	2.58	2.58
	Mean	1.76	1.9	2.33	2.27	2.31	2.3
	S.D.	0.4	0.13	0.18	0.27	0.18	0.16

Lower molars. The DP_4 is a rectangular tooth slightly enlarged distally. This premolar shows a great variation of morphology related to the wear stages. The youngest specimens show a small anterior median sinus and the DP_4 is divided into two lobes by an external oblique sinus and a very small internal sinus. On the lingual distal part, some more mature individuals show an enamel fold that isolates a small island (Fig. 2). This island is, on other specimens, related to the second lobe of the tooth making an intermediate loph reminiscent of some phiomorphs. The latter structure is only seen in a few examples. Another variation occurs in some specimens, where the lingual sinus is very deep and the enamel island is linked to the second lobe.

The M_1 is more squared than the DP_4. The anterior lobe is equal to the posterior one. The external and internal sinuses are almost the same size and are transverse. The anterior wall is rectilinear, whereas the posterior one is very convex. The M_2 is larger than the M_1. The external sinus is slightly more developed than the internal. Both sinuses almost meet in the central part of the tooth. The anterior and posterior walls are convex. The anterior part of the tooth is wider than the posterior one. The M_3 is composed of one or two lobes—with a higher proportion being bilobated. The anterior lobe is the widest, and the second lobe is round and separated from the first by the internal and external sinuses that join in the centre part of the tooth (Fig. 3B–F).

Comparison of Bathyergus hendeyi *with modern and fossil Bathyergidae*

Comparison with modern Bathyergus *species*

The two modern species of *Bathyergus* are distinguished essentially by their size, *B. janetta* being smaller than *B. suillus* s.l. They also show a different arrangement of the back of the skull and the tympanic bullae (De Graaff 1985). The population of *B. suillus intermedius* from Klaver (Cape Province) is characterized by a slightly smaller size (Roberts 1926) than *B. suillus*, but is larger than *B. hendeyi* sp. nov.

The comparison of skulls and mandibular characteristics of *B. hendeyi* sp. nov. with the modern species shows some differences. The angulation of the zygomatic arch is more open in *B. hendeyi* sp. nov. The infraorbital foramina are larger in the fossil species. The upper incisors reach the level of the DP^4–M^1 in modern specimens, whereas they reach the level of the M^{12} in the Langebaanweg form. The skulls from Langebaanweg are higher in their anterior part than in modern *Bathyergus* species, in which the muzzle is very low. In dorsal view, the nasals of *B. hendeyi* show an anterior expansion similar to those of *B. janetta*, whereas in *B. suillus* s.l. the nasals are more rectilinear.

The mandible of the modern *Bathyergus* species differs from those of *Georychus* and *Cryptomys* in showing a large space behind the tooth row between the M_3 and the beginning of the coronoid process. The foramen situated in this space is round and deep. The latter characteristics are also found in *B. hendeyi*.

Bathyergus hendeyi sp. nov. has low-crowned molars in which the roots are always visible, whereas in *B. suillus* the roots are fused and unrecognizable. In molars of *B. janetta* traces of roots can be seen. In the modern species of *Bathyergus*, the four jugal teeth have, in general, the same proportions, whereas

TABLE 2

Measurements (in mm) of mandibular and dental parameters of *Bathyergus hendeyi* sp. nov. and those of modern species. Some measurements of the dental rows are taken directly from Roberts (1951); in the case of *B. suillus intermedius* all measurements are from this source, except for a single specimen from the Transvaal Museum. Abbreviations: QSM—Quartzose Sand Member; 3AN and 3AS—Pelletal Phosphorite Member levels 3AN and 3AS; n—number of individuals; S.D.—standard deviation; WINC—width of the upper incisor; H–DP$_4$—height of the external part of the mandible just below the alveola of the DP$_4$; DP^4–M^3—length of upper jugal teeth row; DP$_4$–M$_3$—length of lower jugal teeth row.

		Bathyergus hendeyi			*Bathyergus suillus suillus*	*Bathyergus suillus intermedius*	*Bathyergus janetta*
		QSM	3AN	3AS			
WINC	n	4	0	1	8	1	3
	Minimum	3.25	—	2.6	3.3	3.37	2.6
	Maximum	3.65	—	—	4.7	—	2.92
	Mean	3.43	—	—	3.93	—	2.73
	S.D.	0.17	—	—	0.5	—	0.17
H–DP$_4$	n	23	9	9	8	1	3
	Minimum	8	9.6	9.9	14	16.1	11.5
	Maximum	13	15	13.7	18	—	12
	Mean	10.9	12.5	13	16.2	—	11.7
	S.D.	0.18	0.17	0.07	0.13	—	0.03
DP^4–M^3	n	8	1	1	22	7	7
	Minimum	7.5	8.3	7.7	10.5	8.3	7.5
	Maximum	8.2	—	—	12	10	10
	Mean	8	—	—	11.2	9.3	8.4
	S.D.	0.5	—	—	0.6	0.6	0.76
DP$_4$–M$_3$	n	21	7	6	8	1	3
	Minimum	8.2	8.75	8.15	10.5	10	8.5
	Maximum	10.3	10.6	10.6	13.2	—	9.55
	Mean	9.1	9.6	9.9	12.1	—	9.1
	S.D.	0.5	0.6	0.4	0.9	—	0.5

in *B. hendeyi*, the M^3 and the DP$_4$ are the smallest teeth (Table 1). The mean lengths of the upper and lower dental rows and the height of the mandible under the DP$_4$ (Table 2) are smaller in *B. hendeyi* than in *B. suillus*, and show similar variation in size to that recorded in *B. janetta* (Figs 5, 6). The t-tests gave highly significant results for the comparisons between *B. hendeyi* and the two subspecies of *B. suillus*— *B. suillus suillus* and *B. suillus intermedius*, and non-significant results between *B. hendeyi* and *B. janetta*. However, the size variation in modern specimens of *B. janetta* is not well known. The width of the upper incisor of *B. hendeyi* is intermediate between those of *B. suillus* and *B. janetta*.

The molars of modern and fossil *Bathyergus* species are not very different, except for the length of the DP_4 (Fig. 6). This tooth is more elongated in the two modern species than in *B. hendeyi*, but there is a great variation in size and shape of the molars during the life of these molerats.
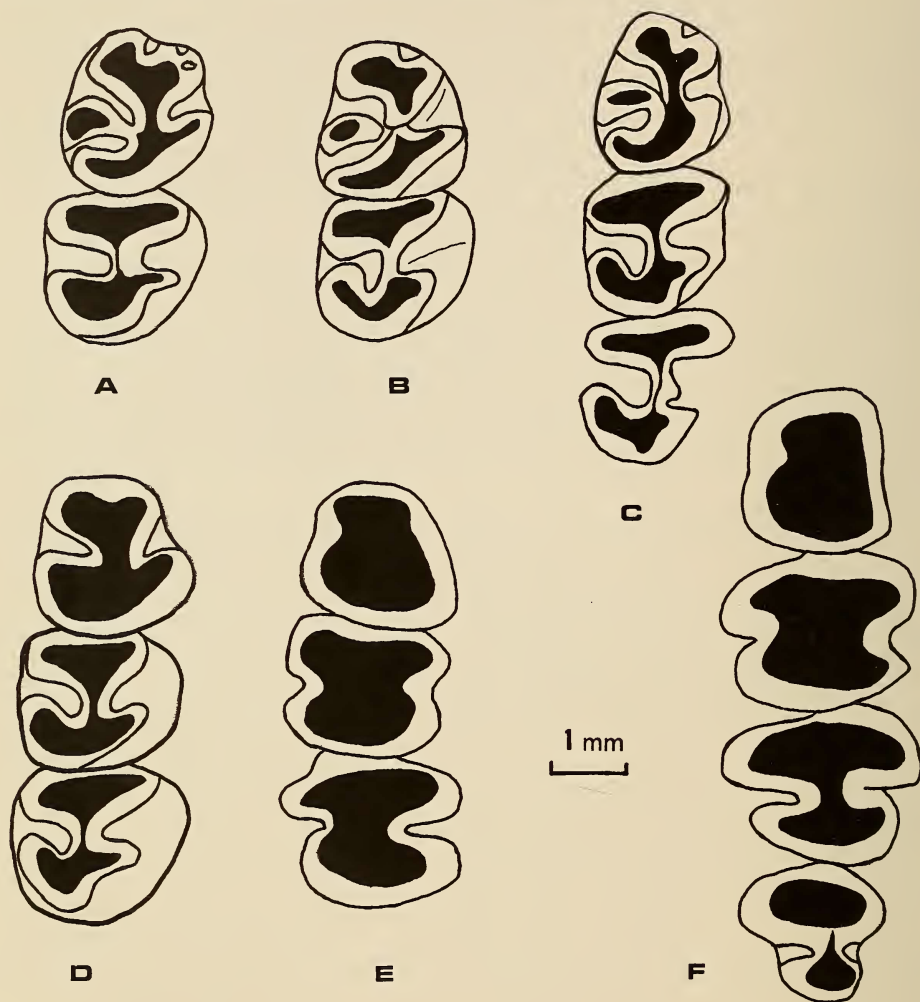

Fig. 4. *Bathyergus hendeyi* sp. nov. Morphological variation during wear in molars. A. Stage 1: right mandible (two molars) with DP_4–M_1; the DP_4 shows two internal sinuses and a single external one. B. Stage 1: right mandible with DP_4–M_1 the internal sinuses isolate an enamel island. C. Stage 2: on teeth more worn than in stage 1, the germ of M_2 shows two lobes separated by a narrow longitudinal crest. D. Stage 3: only one internal sinus and one external one; no trace remains of the enamel island and the M_2 is well developed. E. Stage 4: the teeth are worn and the internal sinus is small, whereas the external one has disappeared on the DP_4. On M_{12} the sinuses are less marked than in the previous stage. F. Stage 5: there is the development of a small M_3 made of two lobes separated by a longitudinal crest; two sinuses divide the tooth in two parts, the posterior one being the narrowest. Scale bar = 1 mm.

Comparison with the fossil Gypsorychus

The upper teeth of *Gypsorychus darti* Broom, 1934, and *G. minor* Broom, 1948, differ considerably from those of *B. hendeyi* sp. nov., and are also very different from all known modern Bathyergidae. They are high crowned and have a greater width than length. The molars are unfolded, except the upper M^3, which consists of two lobes (Broom 1937). In *Gypsorychus* the M^3 is the longest tooth in the dental row, whereas in *B. hendeyi* and most other southern African Bathyrgidae (except *Georychus*) the M^3 is the smallest. According to Broom (1948), the skull of *Gypsorychus* is as large as that of *Bathyergus* and he concluded that the affinities of *Gypsorychus* lay with *Cryptomys*. Present observations confirm that *Gypsoychus* does not share common characteristics with *B. hendeyi* or *Cryptomys*.
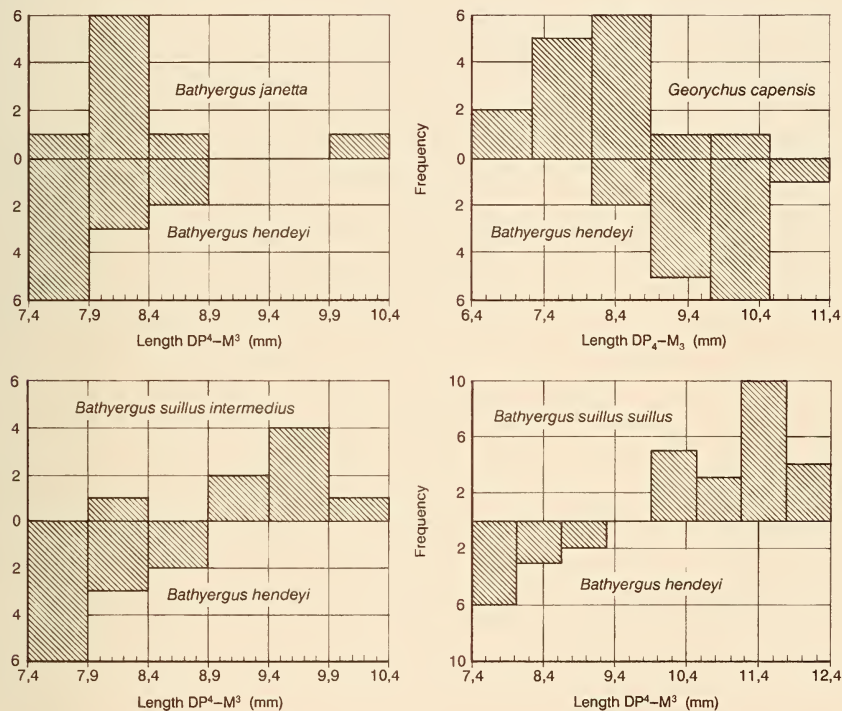

Fig. 5. Comparisons of *Bathyergus hendeyi* sp. nov. with modern species of *Bathyergus* and *Georychus capensis*. Frequency histograms of DP^4–M^3. Axes: abscissa = length in mm; ordinate = frequencies.

Discussion

Whereas no morphological differences are seen between the molars of *Bathyergus hendeyi* sp. nov. found in QSM and PPM levels, there are indications of size differences (Table 1). The *B. hendeyi* specimens from the QSM level are slightly smaller in size and more frequently show traces of supplementary sinuses on the DP_4 than their homologues of the PPM level. This
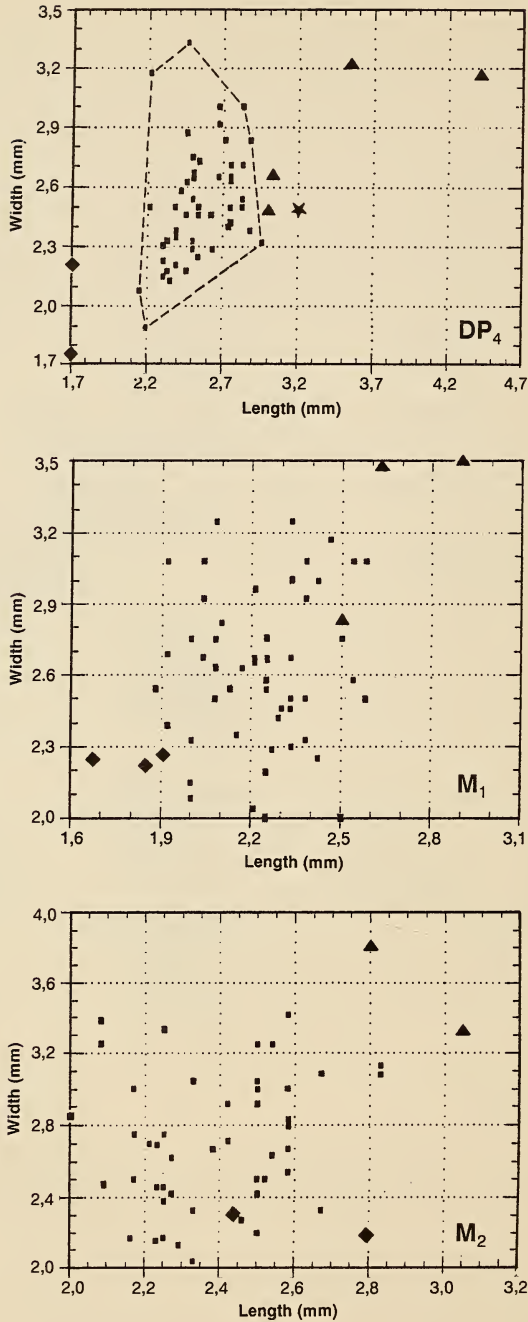
Fig. 6. Scatterplot of the DP$_4$, M$_1$ and M$_2$ molars of modern and fossil species of *Bathyergus* and comparison with *Georychus capensis*. Symbols: ■—*B. hendeyi* sp. nov. from Langebaanweg, ✦—*B. janetta*; ▲—*B. suillus*; ◆—*G. capensis*. Measurements in mm. Axes: abscissa—length; ordinate—width.

could indicate a tendency towards an increase in general size and simplification of the molars with time in the *Bathyergus* lineages.

Bathyergus hendeyi sp. nov. may represent a common ancestor to *B. suillus* and *B. janetta*. Among the species of the genus *Bathyergus*, evolutionary tendencies could be expressed by the increase of the size of skulls and teeth, diminution in the height of the skull, simplification and elongation of the DP_4, and increased hypsodonty.

Bathyergus janetta shares with *B. hendeyi* enlarged nasals and almost identical length of upper and lower dental rows, which could indicate relatively close affinities. However, these characteristics may also be primitive for the genus. In the absence of intermediate fossils, the relationships between modern and fossil species remain unclear.

At 5–4 Ma, *Bathyergus* is well differentiated from other bathyergids, which supports its position in a separate subfamily following Roberts (1951) and suggests a rather early differentiation (around 12 Ma) of the genus, as suggested by molecular trees (Nevo *et al.* 1987) (Fig. 1). However, *Bathyergus* cannot be related directly to a Miocene ancestor due to the gap in the fossil record between 12 and 5 Ma. Moreover, in his study of lower Miocene bathyergids, Lavocat (1973) did not suggest any ancestor to *Bathyergus* among fossil genera and the origins, as well as the age of its divergence, remains unknown.

On the contrary, the suggested age of 2.5 Ma, as determined by the molecular hypotheses, for the divergence between *B. janetta* and *B. suillus* from ancestral *B. hendeyi* is highly probable according to the dental morphology of the fossil examined here.

Genus *Cryptomys* Gray, 1864

One extant species of *Cryptomys* is found in the south-western Cape region—*C. hottentotus* Lesson, 1826 (the common molerat). Within this species Honacki *et al.* (1982) recognized a further five subspecies in *C. hottentotus* s.l. These are *C. h. bocagei*, *C. h. damarensis*, *C. h. darlingi*, *C. h. holosericus*, and *C. h. natalensis*. Recent examination of the karyotypes of the South African bathyergids has shown (Nevo *et al.* 1985) that *Cryptomys*, traditionally considered as monospecific, could comprise at least three distinct forms. These are *C. hottentotus hottentotus* (2N = 54), *C. hottentotus natalensis* (2N = 54) and *C. h. damarensis* (2N = 74 and 78). The study of mtDNA, allozyme and chromosomal variation among the three subspecies of *C. hottentotus* suggested that *C. h. damarensis* should be raised to specific rank (Honeycutt *et al.* 1987). According to Roberts (1951), *C. damarensis* is distinguished by a perforation at the front edge of the orbit (antorbital foramen) that is smaller and not as oblong (being only a little higher than wider) than in *C. hottentotus*. The subspecific status of *C. hottentotus hottentotus* and *C. hottentotus natalensis* is retained at present, despite some genetic differences. In the absence of morphological revision and good external criteria, the term *C. hottentotus sensu lato* (s.l.) will be employed in this paper to designate modern representatives of *C. hottentotus*. Woods (1993) included the subspecies *darlingi*, *holosericus* and *natalensis* in *C. hottentotus*.

Fossil *Cryptomys* are relatively abundant in the Plio–Pleistocene Transvaal caves. Broom (1937) described *C. robertsi* from the Plio–Pleistocene bone breccia at Krugersdorp, near Pretoria (Gauteng Province). Pocock (1987) reported the coexistence of two species at Kromdraai and Sterkfontein: *Cryptomys* cf. *C. hottentotus natalensis* and a larger species, *C. robertsi* Broom, 1937. Pocock (1987) also recorded *Cryptomys* cf. *C. hottentotus* in all sites at Makapansgat, these specimens being smaller than *Cryptomys* cf. *C. h. natalensis* from Sterkfontein. These forms have not yet been described in detail.

Cryptomys broomi sp. nov.
Figs 3E–F, 7

In addition to the numerous remains of *Bathyergus* found at Langebaanweg, a small bathyergid with ungrooved molars and four cheek-teeth has been found. Represented only by a small number of mandibles associated with the teeth, this bathyergid shows a very large diastema and few markedly hystricognathous characteristics of modern *Cryptomys* species, as well as the absence of sinuses on the molars. The existence of an M_2 of nearly identical size to the M_1 differentiates this small bathyergid from Langebaanweg from *Georychus*, and the constant number of 4 cheek-teeth permits separation of the fossil from the modern genus *Heliophobius* that has 2 to 6 cheek-teeth.

Etymology
This species is named in honour of Dr Broom who first paid attention to the rodents of South African Plio–Pleistocene caves.

Material
Holotype. SAM–PQL24012 in the South African Museum (Cape Town). Mandible with DP_4–M_3 from the Quartzose Sand Member (QSM) of the Varswater Formation in East Stream Elephant site of 'E' Quarry at Langebaanweg (Fig. 3F).

Other material
QSM: 1 left mandible fragment with DP_4–M_3; 3 left mandible fragments with DP_4–M_2; 1 right mandible fragment with DP_4–M_2; 1 left and 1 right maxillary fragments with DP^4; 2 right mandible fragments with M_1; 1 left mandible fragment with M_1; 2 right mandible fragments with M_{12}; 1 left and 1 right mandible fragments without molars.
PPM: 1 left mandible fragment with M_{23}; 1 right mandible with M_{23}; 1 left mandible fragment with M_{13}; 1 right mandible fragment with DP_4–M_2; 1 right mandible fragment with M_{12}; 1 right mandible fragment with DP_4–M_1; 3 right and 3 left mandibles with M_1; 3 mandible fragments without molars.

Diagnosis
Cryptomys with low-crowned molars, showing traces of cusps, and similar in size to the molars of *C. damarensis*, *C. hottentotus* s.l. and *C. robertsi*.

Differentiated from *C. hottentotus* s.l. by a narrower angle of the mandible (90°), by a more robust mandible, and by lower crowns. Differentiated from *C. robertsi* by lower crowns and more visible traces of cusps. Differentiated from *C. damarensis* by the slightly larger molars, especially the DP_4, and by lower crowns.

Description of the molars

Measurements are given in Tables 3 and 4.

DP_4 is small, rather rounded and not elongate, with shallow internal and external sinuses. There is a frontal, median, anterior sinus. When the tooth is worn the internal sinus disappears. This premolar has two roots, one anterior to the other (Fig. 3E, F).

M_1 is more squared and slightly larger than DP_4, with an external sinus more developed than on DP_4. The internal sinus is marked but no more deep than on DP_4. On worn teeth, the internal sinus disappears first, followed by the external sinus (Fig. 3E, F).

On M_2, the external sinus is more developed than on the M_1 and almost reaches the centre of the occlusal surface, dividing the molar into two lobes. The first lobe is wider than the posterior one. The internal sinus may be either less developed than on the M_1 or absent (Fig. 3E, F).

M_3 comprises two lobes, well separated by the deep external sinus, and is more elongate than M_1. The second lobe is narrower than the first. There are three roots, two anterior and one posterior (Fig. 3E, F).

TABLE 3

Dental measurements (in mm) of *Cryptomys broomi* sp. nov. (n—number of individuals; S.D.—standard deviation; min.—minimum value; max.—maximum value).

Tooth		Length				Width			
	n	Min.	Max.	Mean	S.D.	Min.	Max.	Mean	S.D.
DP_4	3	1.5	1.58	1.54	0.04	1.75	1.83	1.79	0.04
M_1	6	1.29	1.79	1.43	0.18	1.66	2.17	1.88	0.17
M_2	4	1.4	1.75	1.62	0.15	1.75	2.00	1.85	0.12
M_3	2	1.3	1.66	—	—	1.05	1.75	—	—

Comparison of Cryptomus broomi *with modern and fossil Bathyergidae*

Comparison between modern and fossil Cryptomys

Cryptomys and other bathyergids are well known for the extreme variability in size and shape of their jugal teeth during growth (Taylor *et al.* 1985; Denys 1988) and for having teeth that do not erupt simultaneously. This renders comparison very difficult, because *Cryptomys broomi* sp. nov. is represented by only a few specimens. Comparison of molar dimensions shows that *C. broomi* has variation similar to that found in modern *C. hottentotus* s.l. and *C. robertsi* from Kromdraai B and Sterkfontein sites. The small Langebaanweg *Cryptomys*

sample shows as much variability as in all other modern and fossil represen-
tatives of the genus (Tables 3, 4). Comparison of the length of DP_4 of four
species of *Cryptomys* (Fig. 7) shows that *C. broomi* is slightly larger than
C. damarensis. The length of the lower dental row is very similar to that of the
specimens of *C. hottentotus* s.l. and *C. damarensis* (Table 4). The t-tests gave
non-significant differences between *C. hottentotus*, *C. damarensis* and
C. broomi at the 95 and 99 per cent levels.

From a morphological point of view, the most striking trait of *C. broomi* sp.
nov. is the low-crowned teeth. Roots of teeth are seen in all *C. broomi*
specimens, whereas they remain invisible in *C. robertsi* and all modern
Cryptomys, which have higher crowns.

Some juvenile specimens from Langebaanweg retain more clearly a trace of
cusps on their molars, especially the lower M_3 of the type specimen. The M_3
is very wide anteriorly compared to other species of *Cryptomys*. Modern and
fossil *Cryptomys* share the same shape and disposition of the mandible with a
long and transverse symphysial joint and a small diastema; however, this
character is highly variable. The incisors of *C. broomi* sp. nov. are less
straightened and the wear facets more oblique than in *C. hottentotus* s.l. and
C. damarensis.

Comparison of Cryptomus broomi *with modern* Georychus capensis

Georychus capensis has a more robust mandible than *C. broomi* sp. nov.
and larger teeth that retain traces of the crests until an advanced stage of wear.
There is no trace of the roots in *G. capensis* and the jugal teeth are relatively
high crowned. In *G. capensis*, the molars increase in size from the M_1 to the
M_3, the M_3 being the largest tooth, whereas in *C. broomi* sp. nov. and other
Cryptomys species the M_3 is the smallest molar (Fig. 7).

Discussion

In the absence of a more detailed morphometric study of the different
modern *Cryptomys* species, any attempt to relate *C. broomi* sp. nov. to one or
other species of the genus remains difficult. The size of the Langebaanweg fossil
places it very close to *C. robertsi* from Plio–Pleistocene sites of Gauteng and
North-West Province. *Cryptomys broomi* shows a plesiomorphic character in
being less high crowned. However, the phylogenetic relationships between
C. broomi and the modern *Cryptomys* cannot yet be established, particularly the
relationship between *C. broomi* and *C. damarensis*.

The presence of a primitive *Cryptomys* at Langebaanweg, aged about
5–4 Ma, can be discussed in the light of the molecular hypotheses of Nevo *et al.*
(1987), summarized in Figure 1. The morphological characteristics of
C. broomi sp. nov. appear primitive and could be interpreted in the following
two ways. In a first hypothesis, from its dental morphology, *C. broomi* is
the common ancestor of *C. hottentotus* s.l. and of *C. damarensis*, and their
divergence occurred after 5–4 Ma. (This differs slightly from the two
hypotheses of Nevo *et al.* (1987), which—in both cases—suggested an earlier
divergence age of *C. damarensis* at 6–5 Ma (Fig. 1A, B)). In the second

TABLE 4

Comparison of DP$_4$-M$_3$ length in four species of *Cryptomys* and in *Georychus capensis*.

		Cryptomys broomi sp. nov.	*Cryptomys robertsi*	*Cryptomys damarensis*	*Cryptomys hottentotus*	*Georychus capensis*
DP$_4$-M$_3$	n	4	1	6	16	17
	Mean	6.4	—	6.2	5.7	8
	Minimum	5.9	5.7	5.5	4.7	6.4
	Maximum	6.6	—	7	6.8	10
	S.D.	0.3	—	0.6	0.6	0.9

hypothesis, *C. broomi* is more closely related to *C. hottentotus* s.l. and was differentiated separately from *C. damarensis*. In the latter case, *C. damarensis* represents another lineage differentiated before or after other *Cryptomys*. However, *C. damarensis* is too close to *C. broomi* to suppose a very early or late differentiation of *C. damarensis*, and the age of 5–6 Ma given by molecular data for its differentiation is acceptable. So far as is known, no fossil of *C. damarensis* has yet been found to support either the dental or molecular hypothesis.

The relationships of *C. broomi* sp. nov. with *G. capensis* must also be discussed here. The comparison of the dental morphology of the two species shows that *Georychus capensis* is very different from *C. broomi* and also from *C. damarensis*, which suggests an earlier differentiation than 5 Ma, contrary to the first suggestion provided by the molecular data of Nevo *et al.* (1987) (Fig. 1A) and supports the second hypothesis of a very early divergence for *Georychus* (Fig. 1B). This corresponds with the results of the mitochondrial DNA data of Honeycutt *et al.* (1987). The absence of *Georychus* from Langebaanweg could be due to ecological or taphonomic reasons rather than phylogenetic ones.

CONCLUSIONS

The description of two distinct and modern Bathyergidae at Langebaanweg has some phylogenetic implications and permits more precise interpretation of parts of the molecular trees that have been proposed. In addition, the study provides calibrations and morphological arguments in support of one or other of the hypotheses proposed by Nevo *et al.* (1987).

Firstly, the fact that the two bathyergid genera of Langebaanweg are modern ones, supports Nevo *et al.*'s (1987) hypotheses that the differentiation between *Cryptomys* and *Bathyergus* occurred before 5–4 Ma. However, the lack of a fossil record in upper Miocene times precludes a precise determination of the age of their divergence at the generic level.
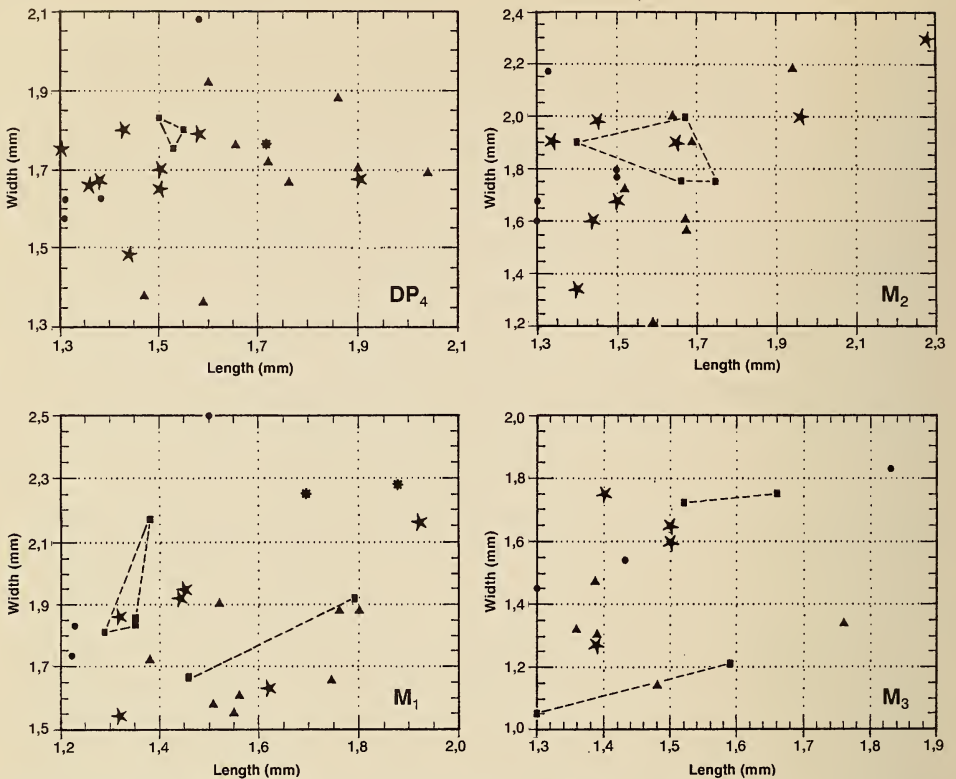
Fig. 7. Scatterplot of DP_4 and M_1 measurements in modern and fossil species of *Cryptomys*. Symbols: ✳ — *G. capensis*; ■ — *C. broomi* sp. nov. from Langebaanweg; ● — *C. damarensis*; ▲ — *C. hottentotus* s.l.; ✶ — *C. robertsi*. Measurements in mm; abscissa — length; ordinate — width.

At the specific level, the fossil record is better documented and the study of dental morphology supports the molecular hypotheses. The small size of *Bathyergus hendeyi* sp. nov. from Langebaanweg and its many primitive characteristics make it a good ancestor to either *B. suillus* or *B. janetta*. This supports Nevo *et al.*'s (1987) age of 2.5 Ma for the divergence of the two modern species. Indeed, examination of the *Bathyergus* skull from the Elandsfontein site (1–0.3 Ma) (Pleistocene) shows that it is clearly *B. suillus*. Moreover, the study of different South African rodent lineages has shown that the time period around 2.5 Ma corresponds to different speciation events (Denys 1990).

The *Cryptomys broomi* sp. nov. from Langebaanweg is, according to present knowledge, the oldest known representative of the genus *Cryptomys*. It has some primitive characteristics and seems to be relatively closely related to either *C. hottentotus* s.l. or *C. damarensis*. *Cryptomys broomi* could be the ancestor of modern *C. hottentotus* s.l. and could be closely related to the fossil *C. robertsi* (whose specific attribution needs careful revision). *Cryptomys damarensis* is also very closely related to *C. broomi*. In the absence of fossils of *C. damarensis*, it is difficult to determine if this species arose from a lineage

other than the *C. broomi*—*C. robertsi* one or to assess the precise age of its specific divergence.

The study of the oldest *Cryptomys* and *Bathyergus* representatives of the lower Pliocene site of Langebaanweg provides some information on relationships of the South African bathyergids. Despite the lack of intermediate fossils, it is clear that *Cryptomys* and *Georychus* are distinct. On evidence from dental and skull morphology, *Georychus* appears to be relatively distant from *Bathyergus*. The hypothesis of a rather early differentiation of *Georychus* is supported by dental anatomy, as well as the molecular data of Nevo *et al.* (1987) (see Fig. 1B) and of Honeycutt *et al.* (1987). The examination of the Miocene bathyergids shows that, according to Lavocat (1973), the best ancestor of the modern *Georychus–Heliophobius* group could be *Proheliophobius*. The revision of the numerous species of Miocene Bathyergidae from East and South Africa should provide further information concerning the origin of the first *Bathyergus*. The relationships of the Pliocene genus *Gypsorychus* remain to be studied, and it is clear that the family Bathyergidae shows a more complex history and evolutionary scenario than the systematics of modern Bathyergidae has led us to understand.

ACKNOWLEDGEMENTS

REFERENCES

BROOM, R. 1934. On the fossil remains associated with *A. africanus*. *South African Journal of Science* **31**: 471–480.

BROOM, R. 1937. On some new pleistocene mammals from limestone caves of the Transvaal. *South African Journal of Science* **33**: 750–768.

BROOM, R. 1939. The fossil rodents of the limestone cave at Taungs. *Annals of the Transvaal Museum* **19** (3): 315–317.

BROOM, R. 1948. The giant rodent mole *Gypsorychus*. *Annals of the Transvaal Museum* **21** (1): 47–49.

DENYS, C. 1988. Nouvelles observations de la structure dentaire de spécimens juvéniles de *Cryptomys hottentotus* (Bathyergidés, rongeurs). *Mammalia* **52** (2): 292–294.

DENYS, C. 1990. Implications paléoécologiques et paléobiogéographiques de l'étude de rongeurs plio-pléistocènes d'Afrique orientale et australe. Thèse de Doctorat d'Etat. *Mémoires de l'Institut des Sciences de la Terre de l'Université Pierre et Marie Curie, Paris* **6** (90-07): 1–428.

DE GRAAFF, G. 1960. A preliminary investigation into the mammalian microfauna in Pleistocene deposits of caves in the Transvaal system. *Palaeontologia africana* **7**: 79–118.

DE GRAAFF, G. 1975. Family Bathyergidae. Part 6.9: 1–5. *In:* MEESTER, J. & SETZER, H. W. *The mammals of Africa: an identification manual.* Washington: Smithsonian Institution.

DE GRAAFF, G. 1981. *The rodents of southern Africa.* Durban, Pretoria: Butterworths.

GRAY, J. E. 1864. Notes on the species of sand-moles (*Georychus*). *Proceedings of the Zoological Society, London* **1864**: 123–125.

HENDEY, Q. B. 1981. Palaeoecology of the late Tertiary fossil occurrences in 'E' Quarry, Langebaanweg, South Africa and a re-interpretation of their geological context. *Annals of the South African Museum* **84** (1): 1–104.

HONACKI, J. H., KINMAN, K. E., KOEPPL, J. W. 1982. *Mammal species of the world.* Lawrence, Kansas: Allen Press Inc. and The Association of Systematics Collections.

HONEYCUTT, R. L., EDWARDS, S. V., NELSON, K. & NEVO, E. 1987. Mitochondrial DNA variation and the phylogeny of African molerats (Rodentia: Bathyergidae). *Systematic Zoology* **36** (3): 280–292.

LAVOCAT, R. 1973. Les rongeurs du Miocène d'Afrique orientale. 1–Miocène inférieur. *Mémoires et Travaux de l'E. P. H. E. Inst.*, Montpellier **1**: 1–284.

LAVOCAT, R. 1989. Ostéologie de la tête de *Richardus excavans* Lavocat, 1988. *Paleovertebrata, Montpellier* **19** (2): 73–80.

LESSON, R. P. 1826. Voyage autour du monde executé par ordre du roi sur la corvette de S.M. La Coquille pendant les années 1822, 1824, et 1825. *Zoologie Atlas*: 166. Paris.

MAIER, W. & SCHRENK, F. 1987. The hystricomorphy of the Bathyergidae, as determined from ontogenetic evidence. *Zeitschrift für Säugetierkunde* **52** (3): 156–164.

MEESTER, J. A. J., RAUTENBACH, I. L., DIPPENAAR, N. J., BAKER, C. M. 1986. Classification of Southern African mammals. *Transvaal Museum Monographs* **5**: 1–359.

NEVO, E., CAPANNA, E., CORTI, M., JARVIS, J. U. M. & HICKMAN, G. C. 1985. Karyotype differentiation in the endemic subterranean mole rats of South Africa (Rodentia, Bathyergidae). *Zeitschrift für Säugetierkunde* **51** (1): 36–48.

NEVO, E., BEN-SHLOMO, R., BEILES, A., JARVIS, J. U. M. & HICKMAN, G. C. 1987. Allozyme differentiation and systematics of the endemic subterranean mole rats of South Africa. *Biochemical Systematics and Ecology* **15** (4): 489–502.

POCOCK, T. N. 1976. Pliocene mammalian microfauna from Langebaanweg: a new fossil genus linking the Otomyinae with the Murinae. *South African Journal of Science* **72** (2): 58–60.

POCOCK, T. N. 1987. Plio–Pleistocene fossil mammalian microfauna of southern Africa— a preliminary report including description of two new fossil muroid genera (Mammalia: Rodentia). *Palaeontologia africana* **26** (7): 69–91.

ROBERTS, A. 1926. Some new South African mammals and some changes in nomenclature. *Annals of the Transvaal Museum* **11** (4): 245–263.

ROBERTS, A. 1951. *The mammals of South Africa.* Johannesburg: The Mammals of Africa Book Fund.

SCHREBER, J. C. D. VON. 1782. *Die Säugthiere in Abbildungen nach der Natur mit Beschreibungen* **4**: 715. Erlangen: Walther.

THOMAS, O. & SCHWANN, H. 1904. Diagnosis of *B. janetta. Abstract of the Proceedings of the Zoological Society, London* **1904** (2): 5–6.

TAYLOR, P. J., RAUTENBACH, I. L., DIPPENAAR, N. J. & BAKER, C. M. 1985. Age determination in the Cape molerat *Georychus capensis. South African Journal of Science* **20** (4): 261–267.

WOODS, C. A. 1993. Suborder Hystricognathi. *In:* WILSON, D. E. & REEDER, D. M. *Mammal species of the world. A taxonomic and geographic reference.* (2nd edition). Washington and London: Smithsonian Institution Press.